

and the populations to the east, therefore supporting the opinion that there are two species: *A. olivaceus* in the Philippines, and *A. moluccanus* elsewhere. Two species of bush hen were found on Karakelong Island, in the Talaud Islands of Indonesia. One of these species was identified as *A. moluccanus*, whilst the other, collected on 6 September 1996, is shown to be a new species, the Talaud Bush Hen *A. magnirostris*. The sympatry of *A. magnirostris* and *A. moluccanus* on Talaud is of great interest since this is the only known locality where two apparently ecologically similar species of *Amaurornis* co-exist. Talaud Bush Hen differs from the other bush hen species in having darker underparts with no contrasting paler-coloured undertail-coverts and in its considerably bigger skull and longer, broader bill with a distinctly arched culmen. Its habitat preferences may also differ, being primarily a forest species and occurring in primary forest far from disturbed areas. Vocalisations apparently differ from comparable calls of *A. moluccanus*, although it was not possible to compare these with similar calls of *A. olivaceus*. Prior to the discovery of *A. magnirostris* and the recently described Talaud Rail *Gymnocrex talaudensis*, no undisputed species were known to be confined to Talaud. The existence of two rails possibly endemic to Talaud therefore considerably elevates the conservation value of the islands. Evidence suggests that the Talaud Bush Hen is widespread on the island, where significant areas of suitable habitat still occur. The species is therefore probably not immediately threatened. Nevertheless, since its exact ecological requirements remain unknown, and in view of the proven vulnerability of rails on islands, many of which have become extinct in the past, the Talaud Rail should be considered to be Near-Threatened.

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## Courtship behaviour, vocalizations, and species limits in *Atthis* hummingbirds

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Hummingbirds of the genus *Atthis* were first described scientifically in 1839 by Lesson & DeLatre, based on specimens from Jalapa and Coatepec in central Veracruz, Mexico (*A. heloisa*). Some 40 years later, in 1878, Ridgway described a second form of the genus, *A. ellioti*, from Volcán de Fuego, in the Pacific cordillera of Guatemala. Griscom (1932) subsequently described another southern form *A. "h."* *selasphoroides* from the highlands of Honduras, and Moore (1937) described another northern form *A. h. margarethae* from northwestern Mexico.

Confusion reigned long regarding species limits in the genus. In spite of their original description as a separate species, populations south of the Isthmus of Tehuantepec were included within *A. heloisa* by Baird *et al.* (1874) and Boucard (1892–1895). Since then, opinions have differed about whether *ellioti* deserves recognition as a species, with some authors arguing for conspecificity (e.g. Peters 1945, Johnsgard 1983) and others separating them as two species (e.g. Berlioz 1938, Friedmann *et al.* 1950, AOU 1983). In general, the debate seems to centre on the idea that the two *Atthis* hummingbirds differ only in minor details of colour; given their allopatric distributions, the decision hinged upon taxonomic viewpoint only.

Even the distinctiveness of the genus has been disputed, with the suggestion that it should be merged into *Selasphorus* (Johnsgard 1983), in spite of its perhaps closer relationship with *Stellula* (Ridgway 1892, Wolters 1976, Sibley & Monroe 1990). The close relationship of the genera *Archilochus*, *Atthis*, *Calypte*, *Stellula*, and *Selasphorus*, together with other small, gorgeted hummingbirds is supported by skeletal synapomorphies, but little resolution of relationships has been possible within the clade (R. L. Zusi pers. comm.). Howell & Webb (1995) merged *Atthis* into *Selasphorus*, and combined *Archilochus*, *Calypte*, and *Stellula* into *Archilochus* with no comment or justification. We regard this arrangement as preliminary and arbitrary.

Unfortunately, little has been published regarding the ecology, behaviour, and vocalizations of either form of *Atthis*. Especially relevant to the question of species limits, the displays and vocalizations associated with courtship have been described only briefly by Howell & Webb (1995) and Skutch (in Bent 1940). The purpose of the present paper is to present descriptions of the courtship displays and vocalizations of the northern populations of these hummingbirds, compare with descriptions of these displays in southern populations, to point out differences in behaviour and morphology between the two forms, and to comment on implications for their specific status.

### Methods

As part of avifaunal inventory studies, KZ and DAK observed *Atthis* hummingbirds at two localities in cloud forest in the Sierra Mazateca in northern Oaxaca: 29–31 January 1994, at Puerto de la Soledad, a microwave station at the highest point along the road from Teotitlán del Camino to Huautla de Jiménez, Oaxaca (specific locality: Distrito de Teotitlán del Camino, Puerto de la Soledad, GPS coordinates 18°9.951'N, 96°59.891'W, 2280 m); and 21 May–2 June 1994 near San Martín Caballero, a town in an isolated northeastern spur of the Sierra Mazateca (specific locality: Distrito de Teotitlán del Camino, 1 km NE San Martín Caballero, 18°6.721'N, 96°38.426'W, 1470 m). Two specimens were preserved as vouchers [OMVP 1041 (male) and 1130 (female)], deposited at the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México. *A. ellioti* was observed by ATP on 3–10 July 1995 in cloud forest in Parque Nacional Los Andes, Volcán Santa Ana, Departamento de Santa Ana, El Salvador.

To assess differences in vocalizations, we studied recordings of *Atthis* hummingbirds provided by the Cornell Library of Natural Sounds, and compared them to vocalizations heard during our field studies. This material included recordings by Theodore A. Parker III of *A. heloisa* (LNS 17214) from above Puerto Los Mazos, Jalisco, Mexico, and of *A. ellioti* from Cerro Verde, Santa Ana, El Salvador, made by W. A. Thurber.

To provide a preliminary assessment of morphological variation, we examined specimens of both forms in the collections of the University



Figure 1. Distribution of hummingbirds of the genus *Atthis*. Black areas indicate populations of *A. heloisa*; dark grey indicates populations of *A. ellioti*; and light shading indicates probable continuity of populations in appropriate habitats.

of Kansas Natural History Museum, Field Museum of Natural History, Southwestern College, and the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México. In all, we inspected 41 males and 13 females of the northern populations, and 7 males and 2 females of the southern populations. Additional specimen information was kindly provided by the Louisiana State University Museum of Natural Science.

### Distribution

The distribution of *Atthis* hummingbirds generally follows the major mountain systems of northern Mesoamerica (Fig. 1). Populations assigned to *A. h. heloisa* range from central Tamaulipas south in the Sierra Madre Oriental to the Nudo de Zempoaltépetl of northern Oaxaca, in the interior in the vicinity of the Federal District and on Cerro San Felipe in northern Oaxaca, and through the Sierra Madre del Sur of Guerrero and Oaxaca; but the species was not detected on the peripheral montane forest island of Cerro Piedra Larga in east-central Oaxaca (Peterson *et al.* in prep.). An isolated population apparently occurs in southcentral San Luis Potosí in the vicinity of Alvarez; Salvin & Godman (1879–1904) reported a specimen, perhaps of doubtful veracity, collected by A. Dugés in Guanajuato (not

included on map for lack of a more specific locality). A specimen collected by Mario del Toro Avilés at "Montañas Gineta", Oaxaca, is an example of *A. h. heloisa* outside of that form's range, another example of that collector's notoriously unreliable labelling of specimen material (Binford 1989).

Populations referred to as *A. h. margarethae* are restricted to the coastal slopes in Sinaloa, Nayarit, and Jalisco, and then apparently in the Transvolcanic Belt east to western Estado de México. Their absence from the higher peaks of the main body of the Sierra Madre Occidental is odd, given their occurrence in similar habitats in the Transvolcanic Belt. Our limited reexamination of the characters used by Moore (1937) indicated that the differences appear real, although the distributional gap that he mentioned does not, based on ranges outlined in Friedmann *et al.* (1950) and Howell & Webb (1995). Two female specimens described as *A. morcomi* by Ridgway (1898) from southeastern Arizona appear to represent either stragglers or mislabelled specimens; Bangs (1929) pointed out that both fall completely within the range of variation of *A. h. heloisa*. Hummingbirds of this genus have not been found subsequently at the type locality, in spite of its extreme popularity among birdwatchers. Although these extralimital records might suggest seasonal or altitudinal movements, evidence available is insufficient to demonstrate this phenomenon convincingly.

### Courtship behaviour

Observations of courtship behaviour of *A. h. heloisa* were as follows. Males were distributed relatively uniformly through the habitat, especially along ridgetops, frequently perching on high, exposed branches of *Podocarpus* sp. in disturbed vegetation along trails. Females were less obvious, often hidden nearby in dense vegetation closer to the ground. Individuals of both sexes were observed to feed low to the ground from red-flowered *Salvia* sp. (Lamiaceae) at Puerto de la Soledad, and from yellow-flowered *Palicourea galeottiana* (Rubiaceae) at San Martín Caballero.

Males sang from perches, and appeared to be consistent in their use of particular branches, being seen in the same positions on as many as 12 consecutive days. Vocalizations included a rather soft, short *tsil* given by individuals of both sexes. Perched males, however, gave the same *tsil*, followed by a thin whistling *wewewewewewew* that rose and then fell in pitch, lasting a total of two or three seconds (Fig. 2), the whistled portion being reminiscent of songs of *Calypte costae* (Wells *et al.* 1978, KZ pers. obs.). Some immature-plumaged males at San Martín Caballero were heard to sing two or three repetitions of a briefer version of this song in quick succession, much as described by Wells *et al.* (1978) for *C. costae*.

Perched males oriented themselves towards nearby females, which were often perched or foraging. As frequently as once per minute, a male would fly to within 10 cm of a female and hover horizontally in front of her, spreading his gorget and cocking his spread tail vertically

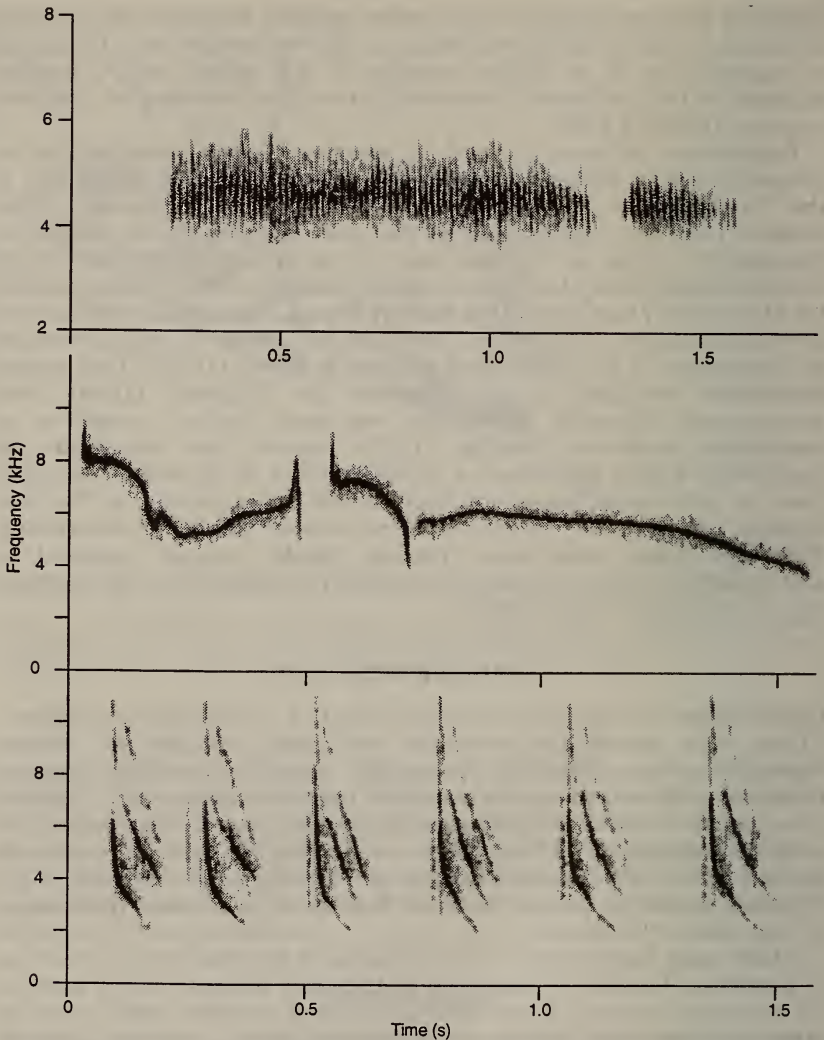


Figure 2. Sounds made by *Atthis* hummingbirds: wing noise (top) and song (middle) of *A. heloisa*, recorded in Jalisco, Mexico; and song of *A. ellioti* (bottom), recorded in El Salvador.

over his back, but was not observed to make any display dive, as do other related genera (Wells *et al.* 1978, Johnsgard 1983). During the hovering, the male's wings produced a wavering thrumming noise (Fig. 2; Robins & Heed 1951), and he often followed the female's movements closely. The noise produced by the wings was similar to that of courting *Selasphorus platycercus*, although somewhat softer (KZ pers.

obs.). Occasionally, while courting females, males flew in horizontal loops as long as 8 m, making the wing noise continuously. The wing noise was also noticeable when males flew in non-courtship behaviours such as foraging, but whether it is always produced during flight is unclear; Howell & Webb (1995) also noted that wing noise is louder during displays, but produced continuously. Immature males were not seen to court females; nor were immature males or females heard to produce wing noise when flying. Observations in January included both singing and courtship, but in May only singing was noted, suggesting that nesting was already well underway or completed.

These observations contrast in some respects with those of Skutch (Bent 1940) of *A. ellioti* in Guatemala and of Thurber *et al.* (1987) from El Salvador. They described assemblies of males spaced 25–30 m apart, with no other such assemblies detected within 2 km. Similar to our observations, the males sang from exposed perches, but their song was described as rising and falling in pitch, more rich and varied (lacking the whistling quality) than in *A. heloisa*, and lasting 30–40 seconds, much longer than in *A. heloisa*, as was borne out by the recordings we studied (Fig. 2). No pronounced wing noise was noted. Excepting the latter point, these differences are largely in accord with descriptions in Howell & Webb (1995). Displaying males apparently moved their gorgets, and often sang while in looping flights, but were not observed to approach the females closely (but see Howell & Webb 1995).

Hence, several marked differences seem to exist in the vocalizations and courtship behaviours of the two forms of *Atthis* hummingbirds. The northern form (*A. heloisa*) sings a simpler song and only while perched, approaches closely to females while in flight, and produces a loud humming wing noise while flying. Observations (ATP) at close range of *A. ellioti* in El Salvador indicated that its wing noise is much quieter and less throbbing than in *A. heloisa*; this observation contradicts a brief mention of display behaviours in Howell & Webb (1995). Finally, and perhaps most interesting, is the possibility that the southern birds display in groups (leks?), whereas the northern birds show no obvious tendency towards clumping; S. N. G. Howell, however, reports observations of clumped and nonclumped displaying males in each form (pers. comm.).

### Morphology

Our examinations of study skins revealed several differences between males of the northern and southern forms of *Atthis*. The inner web of the outermost primary of all adult males of *A. heloisa* examined was notched for an average of 6.5 mm from the feather tip (Fig. 3). No females or immature males showed this modification, nor did any individual examined of *A. ellioti*. This structural modification, noted by Ridgway (1892), probably accounts for the humming noise produced by adult male *A. heloisa* (Monroe 1968). An interesting sidelight of this observation, if the pulses in the noise represent wingbeats (Fig. 2), is that the wingbeat frequency for *A. heloisa* can be calculated at 61.3 beats per second.



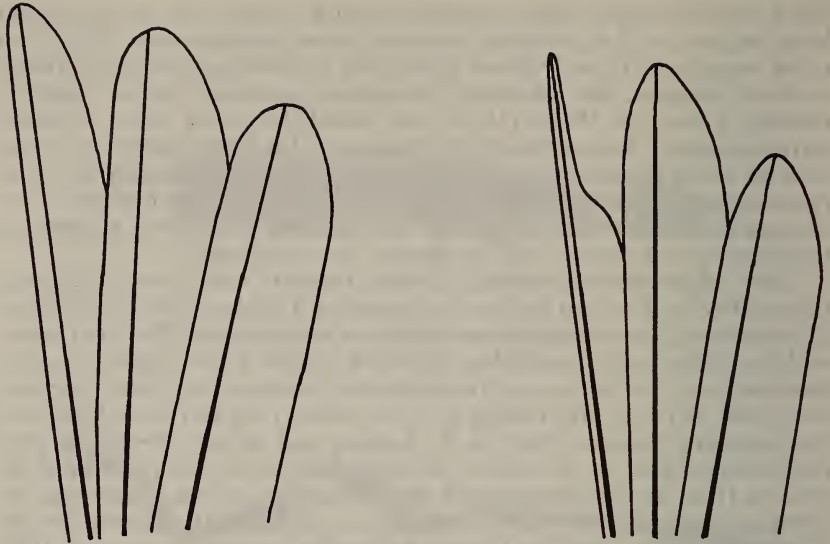


Figure 3. Shape of outer primaries of left wings in *Atthis ellioti* (left, FMNH 42768) and *A. heloisa* (right, KU 46137), both adult males.

This notch of the inner web of the outer primary in *A. heloisa* is the most extreme within the five closely related genera *Selasphorus*, *Atthis*, *Archilochus*, *Calypte*, and *Stellula*. The latter three genera and *Selasphorus flammula* show no notch of the outer primary, whereas *S. platycercus* shows a notch of the distal portion of the feather only. Other *Selasphorus* (*S. rufus*, *S. sasin*, and *S. scintilla*; *S. ardens* not determined) have a pointed outer primary, but no notch.

The colour of the two *Atthis* forms' gorgets differs, in that gorgets of *A. heloisa* are of a rich magenta purple or bluish purple, but those of *A. ellioti* lack blue almost completely and are decidedly more reddish, especially in Honduran *A. e. selasphoroides* (Monroe 1968), even when specimens of similar time since collection are compared. Additionally, the length of the gorgets of adult males may differ, although this feature is difficult to evaluate quantitatively; gorgets of *A. ellioti* seem to be about 3–5 mm longer than those of *A. heloisa*. Our measurements of body dimensions were based on too few individuals to permit statistical testing, but seem generally to support the notion that *A. ellioti* is somewhat smaller than *A. heloisa* in bill and tail length, but slightly larger in wing length, as documented by Ridgway (1892, 1911).

### Species limits

The sum of the information presented above is that the northern and southern forms of *Atthis* differ in several regards. The two forms differ in courtship behaviour, song structure, wing morphology, and